

Phylogenetic analyses of *Paeonia* section *Moutan* (tree peonies, *Paeoniaceae*) based on morphological data

^{1,2}ZHOU Zhi-Qin ¹PAN Kai-Yu ¹HONG De-Yuan*

¹(Laboratory of Systematic and Evolutionary Botany, Institute of Botany, the Chinese Academy of Sciences, Beijing 100093, China)

²(Department of Horticulture, Southwest Agricultural University, Chongqing 400716, China)

Abstract Cladistic analysis of the morphological relationship of 40 populations of *Paeonia* sect. *Moutan* DC. (including all wild species) was carried out with an attempt to have a better understanding of the phylogeny of tree peonies. Twenty-five morphological characters were selected and used in unweighted pair-group method using arithmetic averages (UPGMA), the neighbor-joining (NJ) and the maximum parsimony (MP) tree construction executed with PAUP* program. The topologies of the trees obtained were largely in congruence and topological differences occurred only between MP tree and the other two in a clade comprising five species, *P. suffruticosa*, *P. jishanensis*, *P. qiui*, *P. rockii* and *P. ostii*, which were considered as closely related species based on both morphological and cytological characters. In both NJ and UPGMA trees, all the populations of each species formed a monophyletic clade, and the clades of *P. ludlowii*, *P. qiui* and *P. decomposita* had strong bootstrap supports (>90%), the clades of *P. rockii*, *P. delavayi* had moderate bootstrap supports (>70%), and the clades of *P. suffruticosa*, *P. ostii* and *P. jishanensis* had weak bootstrap supports (51%–70%). In MP tree, however, the corresponding bootstrap values of all the clades mentioned above were generally smaller than those in NJ and UPGMA trees and the populations of *P. delavayi*, *P. ostii* and *P. suffruticosa* failed to form monophyletic clades. Based on the above results, interspecific relationships of wild tree peonies were discussed and a phylogeny of sect. *Moutan* was reconstructed for the first time.

Key words *Paeonia*, *Paeonia* section *Moutan*, morphology, population, phylogeny.

Tree peonies belong to sect. *Moutan* DC. in the genus *Paeonia* L. and are all endemic to China (Pan, 1995). In the past decade, important progresses have been made on the taxonomy of tree peonies (Hong, 1997a, 1997b, 1998; Hong D-Y et al., 1996, 1998a, 1998b; Hong & Pan, 1999a, 1999b; Hong T et al., 1992; Pei & Hong, 1995). However, little work was done on the phylogeny of sect. *Moutan* (Zou et al., 1999). Pei and Hong (1995) considered that *P. qiui* Y. L. Pei & D. Y. Hong is morphologically most closely related to *P. jishanensis* T. Hong & W. Z. Zhao. Hong and his co-workers (Hong et al., 1998a) stated that *P. delavayi* Franch. is most closely related to *P. ludlowii* D. Y. Hong, and the cultivated tree peony (*P. suffruticosa* Andr.) may have been derived from *P. suffruticosa* ssp. *yingpingmudan* D. Y. Hong, K. Y. Pan & Z. W. Xie (Hong et al., 1998b). Using a combined data matrix of both external morphological and pollen characters, Yuan and Wang (1999) built a UPGMA tree of five wild tree peony species,

Received: 3 April 2003 Accepted: 4 July 2003.

Supported by a program of the Chinese Academy of Sciences (Grant No. KSCX2-SW-108) and the National Natural Science Foundation of China (Grant No. 30130030).

* Author for correspondence. E-mail: <hongdy@ns.ibcas.ac.cn>.

i.e. *P. decomposita* Hand.-Mazz., *P. ostii* T. Hong & J. X. Zhang, *P. rockii* T. Hong & J. J. Li, *P. qiui* and *P. jishanensis*, and a hybrid, *P. × yananensis* T. Hong & M. R. Li. Because no bootstrap values were given in their tree, the relationships among the species obviously need to be corroborated. Using RAPD markers of 59 populations from seven wild species, *P. decomposita*, *P. ostii*, *P. rockii*, *P. qiui*, *P. jishanensis*, *P. delavayi* and *P. ludlowii*, and one hybrid, *P. × yananensis*, Zou and her co-workers (Zou et al., 1999) built a UPGMA tree of all the species studied, but the tree produced has a topology not in accordance with that of Yuan and Wang (1999). Recently some very important progresses have been made in studies on phylogeny and hybrid speciation in sect. *Paeonia* using DNA sequences (Sang, 2002; Sang et al., 1995, 1997a, 1997b; Ferguson & Sang, 2001; Tank & Sang, 2001). However, information on interspecific relationships within sect. *Moutan* provided by those studies is still quite limited because of the limited sampling (Sang et al., 1995, 1997b; Ferguson & Sang, 2001; Tank & Sang, 2001). Therefore, the main purpose of the present study is to analyze morphological relationship among the species of sect. *Moutan* using different phylogenetic analysis methods based on population sampling, with an attempt to have a better understanding of the phylogeny of wild tree peonies.

1 Materials and Methods

1.1 Materials

The specimens used in this study were all collected from natural populations, except for *P. suffruticosa* ssp. *suffruticosa* which was a photo of the type stored in the Herbarium, Institute of Botany, the Chinese Academy of Sciences, Beijing (PE). Forty populations (each with three or more specimens) representing all eight species and their corresponding subspecies (Hong & Pan, 1999a) were investigated. In addition, two specimens respectively from the two herbaceous sections of the genus *Paeonia*, *P. brownii* Douglas ex Hooker and *P. lactiflora* Pall., were used as functional outgroups in tree constructions. The origin of the materials used in the study is presented in Table 1.

1.2 Methods

The names of species used in this study follow the classification of *Paeonia* sect. *Moutan* made by Hong and Pan (1999a). Twenty-five morphological characters were selected and used in this analysis for their importance in species delimitation. The characters, their states and code numbers are given in detail in Table 2. NEXUS Data Editor (Version 0.5.0) was used to record raw data and create data matrix for tree-building calculations.

The maximum parsimony (MP), neighbor-joining (NJ), and unweighted pair-group method using arithmetic average (UPGMA) trees were constructed using PAUP* 4.0b4a computer program (Swofford, 2000). During tree construction process, all characters were unordered and equally weighted, with multi-states interpreted as uncertainty and “?” treated as missing information. Parsimony analysis was performed by heuristic search with tree-bisection-reconnection (TBR) of branch

Table 1 Information of populations of species in *Paonia* sect. *Moutan* used in this morphological analysis

No.	Names of populations ¹⁾	Origin	Voucher ²⁾	Determined by
1	<i>lactiflora</i>	Weichang, Hebei	Chengde Team 28	D. Y. Hong
2	<i>brownii</i>	USA	—	D. Y. Hong
3	<i>suffruticosa</i>	Type photo	—	—
4	<i>yinpingmudan-HNSX</i>	Song Xian, Henan	H97010	D. Y. Hong
5	<i>yinpingmudan-AHCH</i>	Chaohu, Anhui	9701	D. Y. Hong
6	<i>jishanensis-SXJS</i>	Jishan, Shanxi	96053, PB89501	D. Y. Hong
7	<i>jishanensis-HNJY</i>	Jiyuan, Henan	H97001, 940220	D. Y. Hong
8	<i>jishanensis-ShXYA</i>	Yan'an, Shaanxi	94008	D. Y. Hong
9	<i>decomposita-KD</i>	Kangding, Sichuan	95080A	D. Y. Hong
10	<i>decomposita-MEK</i>	Barkam, Sichuan	PB85025	D. Y. Hong
11	<i>decomposita-DB</i>	Danba, Sichuan	95050-3B	D. Y. Hong
12	<i>decomposita-JC</i>	Jinchuan, Sichuan	9113003	D. Y. Hong
13	<i>rotundiloba-MX</i>	Mao Xian, Sichuan	PB89701, 95015-2B	D. Y. Hong
14	<i>rotundiloba-LX</i>	Li Xian, Sichuan	9112004	D. Y. Hong
15	<i>rotundiloba-WC</i>	Wenchuan, Sichuan	9111009	D. Y. Hong
16	<i>rotundiloba-HS</i>	Heshui, Sichuan	95017-4-9	D. Y. Hong
17	<i>ostii-ShXHL</i>	Huangling, Shaanxi	H97069	D. Y. Hong
18	<i>ostii-HBBK</i>	Baokang, Hubei	97052A	D. Y. Hong
19	<i>ostii-ShXTBS</i>	Taibaishan, Shaanxi	PB85052	D. Y. Hong
20	<i>ostii-HNNX</i>	Neixiang, Henan	H97021A	D. Y. Hong
21	<i>qiui-HBBK</i>	Baokang, Hubei	H97027	D. Y. Hong
22	<i>qiui-HBSX</i>	Songbai, Hubei	PB85034	D. Y. Hong
23	<i>qiui-HNXX</i>	Xixia, Henan	PB88305	D. Y. Hong
24	<i>taibaishanica-ShXMX</i>	Mei Xian, Shaanxi	H97058	D. Y. Hong
25	<i>taibaishanica-GSTS</i>	Tianshui, Gansu	13	D. Y. Hong
26	<i>taibaishanica-XZ (C)</i>	Xizang (cultivated)	H96051	D. Y. Hong
27	<i>rockii-HBBK</i>	Baokang, Hubei	H97051	D. Y. Hong
28	<i>rockii-HBSBX</i>	Songbai, Hubei	PB88029	D. Y. Hong
29	<i>rockii-HNNX</i>	Neixiang, Henan	H97016-1B	D. Y. Hong
30	<i>rockii-HNSX</i>	Song Xian, Henan	94002	D. Y. Hong
31	<i>ludlowii-ML1</i>	Mainling, Xizang	H96182	D. Y. Hong
32	<i>ludlowii-ML2</i>	Mainling, Xizang	H96014	D. Y. Hong
33	<i>ludlowii-ML3</i>	Mainling, Xizang	H96030	D. Y. Hong
34	<i>delavayi-YNZD</i>	Zhongdian, Yunnan	H97128	D. Y. Hong
35	<i>delavayi-YNLJ</i>	Lijiang, Yunnan	H97095-11	D. Y. Hong
36	<i>delavayi-YNKM</i>	Kunming, Yunnan	H97077-4	D. Y. Hong
37	<i>delavayi-SCDW</i>	Dawu, Sichuan	95063	D. Y. Hong
38	<i>delavayi-SCYJ</i>	Yajiang, Sichuan	95070-3	D. Y. Hong
39	<i>delavayi-SCDK</i>	Panzhihua (Dukou), Sichuan	11458	D. Y. Hong
40	<i>delavayi-SCYY</i>	Yanyuan, Sichuan	97110-3	D. Y. Hong
41	<i>delavayi-XZBM</i>	Bomi, Xizang	379	D. Y. Hong
42	<i>delavayi-XZLZ</i>	Nyingchi, Xizang	3229	D. Y. Hong

1) The names of populations are epithets of the species (subspecies) followed by the abbreviation of the population origin. For example, “*yinpingmudan-HNSX*” means the population of *P. suffruticosa* ssp. *yinpingmudan* from Song Xian, Henan Province. 2) All the vouchers are preserved in PE.

Table 2 Morphological characters, their states and code numbers used in data matrix

No.	Characters	Character states and their code numbers
1	leaf type	tri- or tetra-compound (0); bi- or tri-pinnate (1); biternate (2)
2	leaflet number	more than 35 (0); more than 10 (1); 5–9 (2)
3	shape of leaflets	rounded to elliptic (0); ovate to long-ovate (1); ovate-lanceolate to lanceolate (2)
4	terminal leaflets	entire or rarely lobed (0); cleft less than 1/2 of leaflet length (1); cleft more than 1/2 of leaflet length (2); divided to the base of leaflets (3)
5	lateral leaflets	entire or rarely lobed (0); cleft less than 1/2 of leaflet length (1); cleft more than 1/2 of leaflet length (2); divided to the base of leaflets (3)
6	leaflet apex	rounded to obtuse (0); acute (1); acuminate (2)
7	leaflet base	decurent (0); cuneate (1); broadly-cuneate to rounded (2);
8	leaf indumentum beneath	glabrous (0); hairy only along veins (1); obviously hairy throughout the lower surface (2)
9	flower number	> 1 (0); solitary (1)
10	flowering status	more or less pendent (0); erect (1)
11	bract number	1 (0); 2–3 (1); 4–5 (2)
12	petal number	single (0); double (1)
13	petal color	white (0); yellow (1); pink to red (2); purple (3)
14	spots at petal base	absent (0); red or pink-purple (1); dark purple (2)
15	filament color	white (0); yellow (1); pink to red purple (2)
16	carpel number	> 5 (0); 2–4 (1); 1 or rarely 2 (2)
17	carpel indumentum	glabrous (0); densely hairy (1)
18	stigma color	pale yellow to yellow (0); red (1); purple (2)
19	flower disc	leathery (0); fleshy (1)
20	degree of envelopment of carpels by disc	whole (0); only half of carpels (1); only the base of carpels (2)
21	disc color	white (0); pale yellow to yellow (1); red to purple (2)
22	follicle shape	ellipsoid (0); cylindrical (1); long ovoid (2)
23	root shape	ordinary (0); tuberous (1)
24	reproduction	obligately sexual (0); facultatively vegetative (1)
25	habit	subshrubs (0); herbs (1)

swapping algorithm, the MULTREES, and Accelerated Transformation (ACCTRAN) options. UPGMA and NJ trees were constructed using distance measure of mean character difference. The number of 1000 replicates is used for all bootstrap tests.

2 Results

2.1 Topology of trees and bootstrap support of species clades

The NJ, UPGMA and one of the MP trees are shown in Figs. 1–3. The topologies of the three trees were generally in congruence, and the incongruences only occurred between MP tree and the remaining two in the clade consisting of five closely related species, i. e. *P. suffruticosa*, *P. jishanensis*, *P. qiui*, *P. rockii* and *P. ostii* (Figs. 1–3). In both the NJ and the UPGMA trees, all the populations of each species formed a monophyletic group with bootstrap supports at above 50%. On these two trees, the clades of *P. ludlowii*, *P. qiui* and *P. decomposita* were

Table 3 The data matrix of 42 populations and 25 morphological characters used in tree construction analysis

No.	Names of populations ¹⁾	Code numbers of character states
1	<i>lactiflora</i>	22(012)(23)(23)2010120(03)(01)1(01)001210101
2	<i>brownii</i>	22(01)(23)(23)(02)0001103110021210101
3	<i>suffruticosa</i>	221(12)(01)11011213020110020? 00
4	<i>yinpingmudan-HNSX</i>	221(12)121011203020110020? 00
5	<i>yinpingmudan-AHCH</i>	221(12)121011200020120020? 00
6	<i>jishanensis-SXJS</i>	221(123)1(12)(12)211000201100201110
7	<i>jishanensis-HNJY</i>	22(01)111(12)211100021110020110
8	<i>jishanensis-ShXYA</i>	22(01)211(12)2111032(12)0110020110
9	<i>decomposita-KD</i>	00(01)(12)(01)21011203000010100000
10	<i>decomposita-MEK</i>	000(23)(12)21011(12)0(23)0(01)0000100000
11	<i>decomposita-DB</i>	00(01)3(12)21011203000010100000
12	<i>decomposita-JC</i>	0003111011(12)03000010100000
13	<i>rotundiloba-MX</i>	00(01)(13)(01)1101110300101020(01)000
14	<i>rotundiloba-LX</i>	00(01)(12)111011103001010100000
15	<i>rotundiloba-WC</i>	00(01)1111011103001010100000
16	<i>rotundiloba-HS</i>	000(23)1(12)101110300101010(01)000
17	<i>ostii-HBBK</i>	1120021011000020110020000
18	<i>ostii-ShXHL</i>	2(1+2)2002101120(0+2)020110020000
19	<i>ostii-ShXTBS</i>	22(02)(12)021011200021110020000
20	<i>ostii-HNNX</i>	2221021011200020110020000
21	<i>qiui-HBBK</i>	221101201110(03)120120022? 10
22	<i>qiui-HBSX</i>	221(01)012111103120120022? 10
23	<i>qiui-HNXX</i>	2210012111103120120022? 10
24	<i>taibaishanica-ShXMX</i>	110(12)(12)21211200200100010100
25	<i>taibaishanica-GSTS</i>	1101021211200200100010100
26	<i>taibaishanica-XZ(C)</i>	11011(12)1111200201100010100
27	<i>rockii-HBBK</i>	112202111110(03)210100010000
28	<i>rockii-HBSBX</i>	1120021111100200100110000
29	<i>rockii-HNNX</i>	1120021111100200100010000
30	<i>rockii-HNSX</i>	1120021211100200100010000
31	<i>ludlowii-ML1</i>	2212220000101012001211100
32	<i>ludlowii-ML2</i>	2212220000101012001211100
33	<i>ludlowii-ML3</i>	2212220000101012001211100
34	<i>delavayi-YNZD</i>	221(23)(23)200(01)010(012)1(12)10212(12)0110
35	<i>delavayi-YNLJ</i>	221222001010(23)121011220110
36	<i>delavayi-YNKM</i>	221332000010(13)121021220110
37	<i>delavayi-SCDW</i>	2223320000(12)0(12)(01)210112(12)2110
38	<i>delavayi-SCYJ</i>	2223320010201(01)2102122(02)110
39	<i>delavayi-SCDK</i>	222332001020(123)(01)210212(12)2110
40	<i>delavayi-SCYY</i>	2223320000102221021220110
41	<i>delavayi-XZBM</i>	222(23)(23)20000(12)0102101122(02)110
42	<i>delavayi-XZLZ</i>	222(23)(23)20000(12)0102101122? 110

1) The names of populations are defined the same as in Table 1.

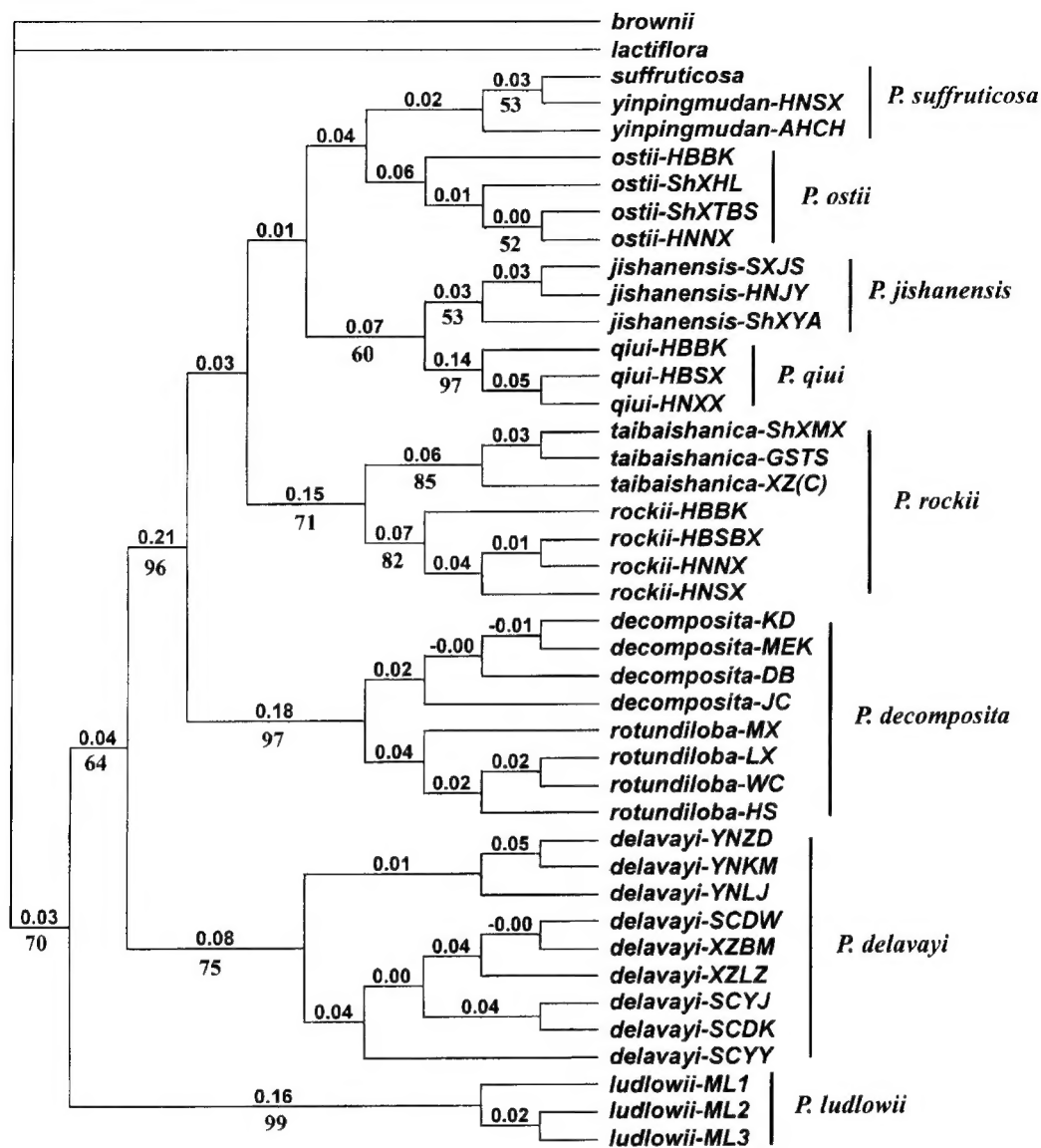


Fig. 1. The unweighted pair-group method using arithmetic averages (UPGMA) tree of the tree peony populations studied in the present analyses. Numbers above branches indicate the mean distance; numbers below branches are bootstrap values.

strongly supported (bootstrap values > 90%), and those of *P. rockii* and *P. delavayi* were moderately supported (bootstrap values > 70%) (Figs. 1, 2). However, in the MP tree, the bootstrap figures of all the species clades were generally smaller than those in the NJ and UPGMA trees and the populations of *P. delavayi*, *P. ostii* and *P. suffruticosa* failed to form their own monophyletic groups (Fig. 3).

2.2 Phylogenetic relationship among species of *Paeonia* sect. *Moutan* DC.

In the trees produced (Figs. 1 – 3), *P. delavayi* and *P. ludlowii* first branched out from the

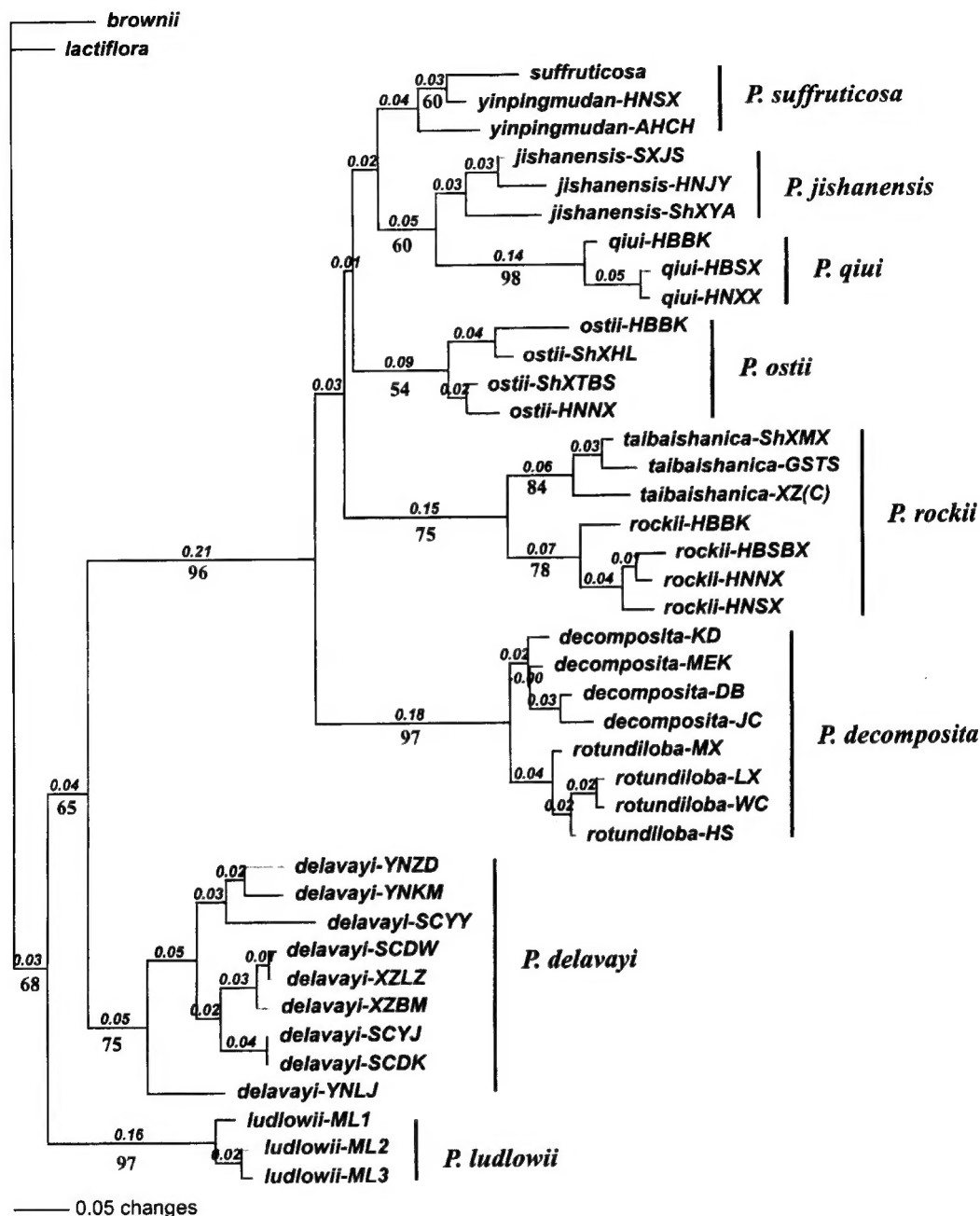


Fig. 2. The neighbor-joining tree of the tree peony populations studied in the present analyses. Numbers above branches indicate the mean distance; numbers below branches are bootstrap values.

other species within sect. *Moutan*. Because the clade was strongly supported by bootstrap values (96% in the NJ and UPGMA trees, 90% in the MP tree), a closer relationship between *P. ludlowii* and *P. delavayi* than between either of them and any other species in sect. *Moutan* was strongly supported. The populations of the two subspecies of *P. decomposita* first formed their own

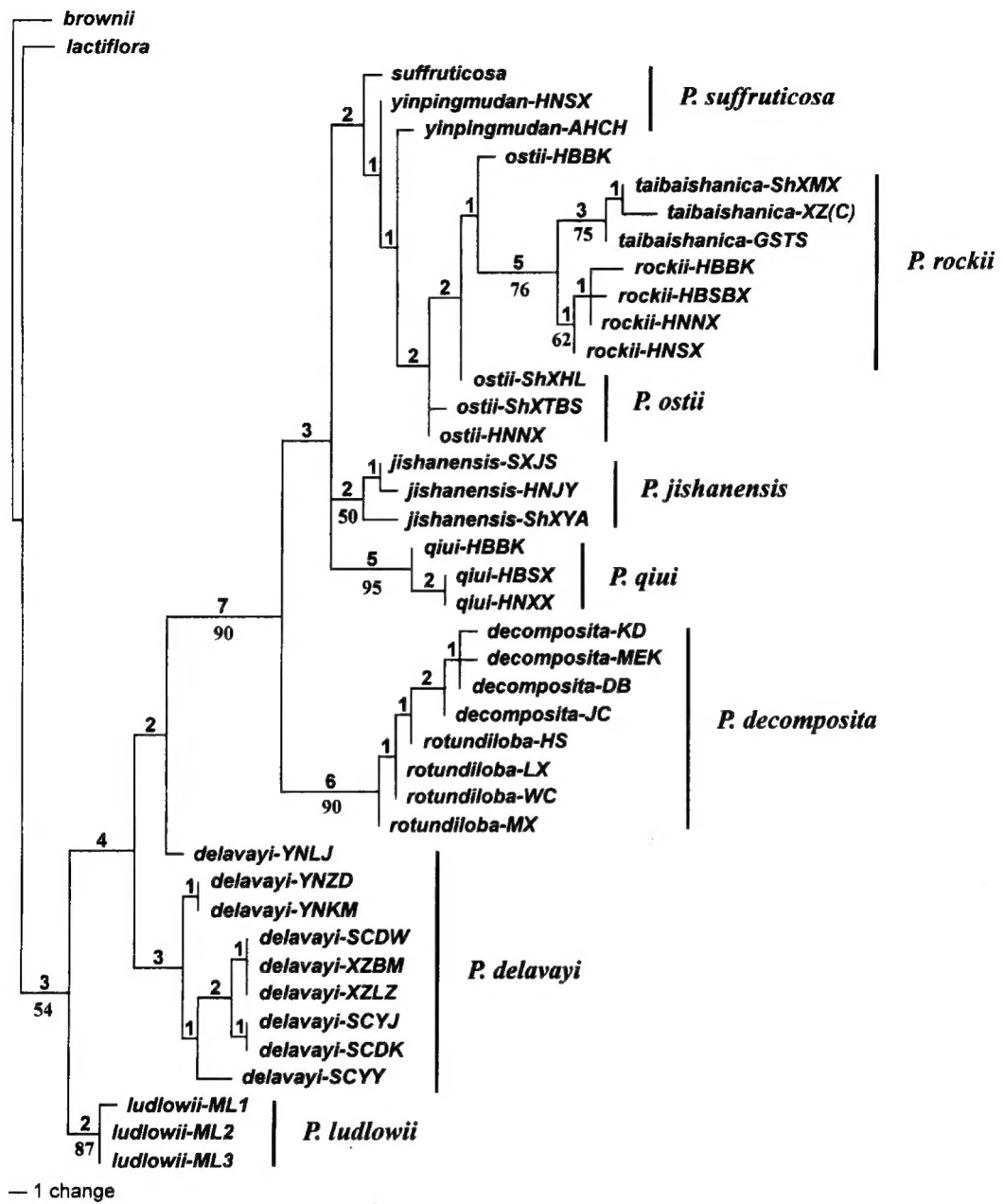


Fig. 3. The maximum parsimony tree of the tree peony populations studied in the present analysis. Numbers above branches indicate the number of character changes that occurred along each branch; numbers below branches are bootstrap values.

monophyletic group respectively (NJ and UPGMA trees), and then together formed a monophyletic clade with a strong bootstrap support (97% in both NJ and UPGMA trees, 90% in MP tree), which in turn consisted of a sister relationship with the clade comprising five species, viz., *P. suffruticosa*, *P. jishanensis*, *P. qiui*, *P. rockii* and *P. ostii*. For this species group, their inter-specific relationships were not well resolved by this analysis because of the topological differences

among the trees obtained and the lack of robust bootstrap support for the branches (Figs. 1–3). The populations of the two subspecies of *P. rockii* formed their own monophyletic groups (bootstrap > 78%), and they then formed a monophyletic clade (bootstrap > 70%) which was sister to the other four species in both the NJ and UPGMA trees (Figs. 1, 2). This sister relationship, however, was not topologically supported by MP tree (Fig. 3). In both the NJ and UPGMA trees, the populations of *P. jishanensis* and *P. qiui* first formed two independent clades, and then joined in a monophyletic group with 60% bootstrap value (Figs. 1, 2), but this group collapsed again in the MP tree (Fig. 3). In addition, the populations of *P. rockii* and *P. ostii* formed a monophyletic group, which was then joined by *P. suffruticosa* in MP tree (Fig. 3). In the same way, these relationships were not supported by both the NJ and UPGMA trees. The relationship among these tree peony species obviously needs further investigation.

3 Discussion

Following de Candolle (1824), Stern (1946) divided the genus *Paeonia* into three sections, sect. *Paeonia*, sect. *Onaepia*, and sect. *Moutan*. The sect. *Moutan*, with four species and two varieties, was further differentiated into two subsections, viz., subsect. *Vaginatae* and subsect. *Delavayanae* (Stern, 1946). Based on a series of field investigations and taxonomic studies on wild tree peonies (Hong, 1997a, 1997b, 1998; Hong et al., 1998a, 1998b; Hong & Pan, 1999b), Hong and Pan (1999a) suggested a new classification system for sect. *Moutan*, in which eight species (with three of them each having two subspecies) were recognized. The present study showed that all the populations of each species in Hong and Pan's (1999a) system formed their own monophyletic clades in all three trees (Figs. 1–3), except for the populations of *P. delavayi* and *P. suffruticosa* in the MP tree, and they together formed a monophyletic group having a sister relationship with the outgroups. Therefore, this result is in consistent with the taxonomic treatment of species in sect. *Moutan* made by Hong and Pan (1999a). In addition, the subdivision of *P. rockii* into two subspecies by Hong (1997a) is also supported in this analysis.

Up to date, our understanding on the phylogeny of sect. *Moutan* was still limited and sporadic (Sang et al., 1995, 1997b; Zou et al., 1999; Yuan & Wang, 1999; Ferguson & Sang, 2001; Tank & Sang, 2001). A close relationship between *P. ludlowii* and *P. delavayi* and their relationship with all the other species in sect. *Moutan* are well recognized by both morphological study (Hong & Pan, 1999a) and molecular evidence (Zou et al., 1999), and are also confirmed by the present analysis. Hong and Pan (1999a) considered that three groups could be distinguished in sect. *Moutan*, with the first group comprising *P. ludlowii* and *P. delavayi*, the second *P. decomposita*, and the third *P. suffruticosa*, *P. jishanensis*, *P. qiui*, *P. rockii* and *P. ostii*. This division implies that *P. decomposita* has an intermediate position among the species of sect. *Moutan*. From Figs. 1–3 we can see that the suggested systematic position of *P. decomposita* is well supported and this result is also consistent with earlier conclusions (Tank & Sang, 2001; Yuan & Wang, 1999).

Previous studies on sect. *Moutan* showed that the interspecific relationships among *P. suffruticosa*, *P. jishanensis*, *P. qiui*, *P. rockii* and *P. ostii* are problematic (Hong & Pan, 1999b; Yuan & Wang, 1999; Zou et al., 1999). These five species were considered to be closely related in both morphological and cytological aspects and were treated as a species complex (*P. suffruticosa* complex) by Hong and Pan (1999b). All the three trees presented in this work (Figs. 1–3) showed that the five species formed a monophyletic clade with *P. decomposita* as its sister group. Pei and Hong (1995) suggested that *P. qiui* is most closely related to *P. jishanensis* and both of them have a close relationship with *P. suffruticosa*. A close relationship between *P. qiui* and *P. jishanensis* is supported by the UPGMA analysis of morphological and palynological data (Yuan & Wang, 1999), but not by molecular evidence (Zou et al., 1999) and only weakly supported by our NJ tree (Fig. 2). In addition, *P. rockii* and *P. ostii* showed a closer relationship than those between either of them and any other species within *P. suffruticosa* complex in both NJ and MP trees (Figs. 2, 3), whereas *P. suffruticosa* showed a closer relationship with *P. ostii* than between *P. rockii* and *P. ostii* in UPGMA tree (Fig. 1). Based on previous works and the present study mentioned above, a phylogenetic relationship among species in *Paeonia* sect. *Moutan* is suggested, as is shown in Fig. 4.

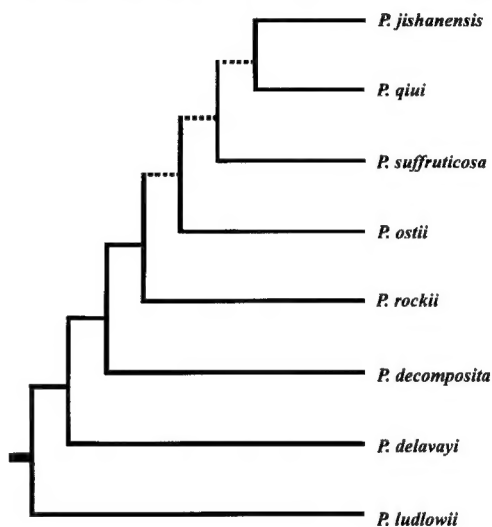


Fig. 4. A suggested interspecific relationship in *Paeonia* sect. *Moutan* DC. The solid lined clades are well supported in the present study and the dotted lined clades need further evidence to confirm.

References

- de Candolle A P. 1824. Prodrum Systematis naturalis Regni vegetabilis. 1: 65–66.
- Ferguson D, Sang T. 2001. Speciation through homoploid hybridization between allotetraploids in peonies (*Paeonia*). Proceedings of the National Academy of Sciences USA 98: 3915–3919.
- Hong D-Y. 1997a. Notes on *Paeonia decomposita* Hand.-Mazz. Kew Bulletin 52: 957–963.
- Hong D-Y. 1997b. *Paeonia* (Paeoniaceae) in Xizang (Tibet). Novon 7: 156–161.
- Hong D-Y (洪德元). 1998. *Paeonia rockii* and its one new subspecies from Mt. Taibai, Shaanxi of China. Acta Phytotaxonomica Sinica (植物分类学报) 36: 538–543.
- Hong D-Y (洪德元), Pan K-Y (潘开玉). 1999a. Taxonomical history and revision of *Paeonia* sect. *Moutan* (Paeoniaceae). Acta Phytotaxonomica Sinica (植物分类学报) 37: 351–368.
- Hong D-Y (洪德元), Pan K-Y (潘开玉). 1999b. A revision of the *Paeonia suffruticosa* complex (Paeoniaceae). Nordic Journal of Botany 19: 289–299.
- Hong D-Y (洪德元), Pan K-Y (潘开玉), Pei Y-L (裴颜龙). 1996. The identity of *Paeonia decomposita* Hand.-Mazz. Taxon 45: 67–69.
- Hong D-Y (洪德元), Pan K-Y (潘开玉), Xie Z-W (谢中稳). 1998b. Yinpingmudan, the wild relative of the king of flowers, *Paeonia suffruticosa* Andrews. Acta Phytotaxonomica Sinica (植物分类学报) 36: 515–520.
- Hong D-Y (洪德元), Pan K-Y (潘开玉), Yu H (虞泓). 1998a. Taxonomy of the *Paeonia delavayi* complex

- (Paeoniaceae). *Annals of the Missouri Botanical Garden* 85: 554–564.
- Hong T (洪涛), Zhang J-X (张家勋), Li J-J (李嘉珏), Zhao W-Z (赵文忠), Li M-R (李明瑞). 1992. Studies on the Chinese wild woody peonies (I): new taxa of *Paeonia* L. sect. *Moutan* DC. *Bulletin of Botanical Research (植物研究)* 12: 223–234.
- Pan K-Y (潘开玉). 1995. The analysis of distribution pattern in the Paeoniaceae and its formation. *Acta Phytotaxonomica Sinica (植物分类学报)* 33: 340–349.
- Pei Y-L (裴颜龙), Hong D-Y (洪德元). 1995. *Paeonia qiui*—A new woody species of *Paeonia* from Hubei, China. *Acta Phytotaxonomica Sinica (植物分类学报)* 33: 91–93.
- Sang T. 2002. Utility of low-copy nuclear gene sequences in plant phylogenetics. *Critical Reviews in Biochemistry and Molecular Biology* 37: 121–147.
- Sang T, Crawford D J, Stuessy T F. 1995. Documentation of reticulate evolution in peonies (*Paeonia*) using internal transcribed spacer sequences of nuclear ribosomal DNA: implications for biogeography and concerted evolution. *Proceedings of the National Academy of Sciences USA* 92: 6813–6817.
- Sang T, Crawford D J, Stuessy T F. 1997a. Chloroplast DNA phylogeny, reticulate evolution, and biogeography of *Paeonia* (Paeoniaceae). *American Journal of Botany* 84: 1120–1136.
- Sang T, Donoghue M J, Zhang D. 1997b. Evolution of alcohol dehydrogenase genes in peonies (*Paeonia*): phylogenetic relationships of putative nonhybrid species. *Molecular Biology and Evolution* 14: 994–1007.
- Stern F C ed. 1946. A study of the genus *Paeonia*. London: The Royal Horticultural Society. 1–146.
- Swofford D L. 2000. PAUP* Phylogenetic Analysis Using Parsimony (* and other methods). Version 4.0b4a. Sunderland: Sinauer Associates.
- Tank D C, Sang T. 2001. Phylogenetic utility of the glycerol-3-phosphate acyltransferase gene: evolution and implications in *Paeonia* (Paeoniaceae). *Molecular Phylogenetics and Evolution* 19: 421–429.
- Yuan T (袁涛), Wang L-Y (王莲英). 1999. Pollen morphology of several tree peony wild species and discussion on its evolution and taxonomy. *Journal of Beijing Forestry University (北京林业大学学报)* 21: 17–21.
- Zou Y-P (邹喻苹), Cai M-L (蔡美琳), Wang Z-P (王子平). 1999. Systematic studies on *Paeonia* sect. *Moutan* DC. based on RAPD analysis. *Acta Phytotaxonomica Sinica (植物分类学报)* 37: 220–227.

芍药属牡丹组基于形态学证据的系统发育关系分析

^{1,2}周志钦 ¹潘开玉 ¹洪德元*

¹(中国科学院植物研究所系统与进化植物学重点实验室 北京 100093)

²(西南农业大学园艺系 重庆 400716)

摘要 对芍药属牡丹组 *Paeonia* L. sect. *Moutan* DC. (全部野生种) 40个居群进行了基于形态学证据的系统学分析, 试图建立组内种间的系统发育关系。利用 PAUP* 计算机程序分别构建了建立在 25 个形态学性状基础上的所有研究类群的距离树 (UPGMA/NJ) 和最大简约树 (MP)。所得树的拓扑结构基本一致, 差异只发生在距离树和简约树之间, 在由形态和细胞学关系都很近的 5 个种 (牡丹 *P. suffruticosa*、矮牡丹 *P. jishanensis*、卵叶牡丹 *P. qiui*、紫斑牡丹 *P. rockii* 和凤丹 *P. ostii*) 构成的分支内部。在距离树 (UPGMA 和 NJ) 中, 每个种的所有居群都首先形成 1 个单系类群, 然后才与其他种的居群相聚。大花黄牡丹 *P. ludlowii*、卵叶牡丹和四川牡丹 *P. decomposita* 3 个种的单系类群得到大于 90% 的自展值支持, 紫斑牡丹和滇牡丹 *P. delavayi* 2 个种的单系类群得到大于 70% 的自展值支持, 牡丹、凤丹和矮牡丹 3 个种的单系类群得到 51%–70% 的自展值的支持。在简约树 (MP) 中, 上述所有种的自展支持值都小于距离树中的相应数值。同时牡丹、滇牡丹和凤丹的全部群体未能形成一个单系群。根据本文的研究结果, 分析讨论并首次提出了野生牡丹的系统发育关系。

关键词 芍药属; 牡丹; 形态学; 居群; 系统发育